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To seek or speak? Dual function of an acoustic signal limits its versatility in communication

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The perception of different attributes of conspecifics is an integral part of intraspecific communication. It can facilitate the recognition of interaction partners or the assessment of potential mates. Acoustic signals can encode fine-scaled information through the interplay of acoustic variability and specificity. A reliable vocal signature is both unique within a class and variable between classes. Therefore, acoustic complexity might be associated with the number of classes to be discriminated. We investigated the assumption that limitations to signal design may affect the communicative functionality of a signal. To do so, we chose a signal with potentially dual functionality which may therefore display such limitations. In bats, echolocation is used primarily for foraging and orientation but there is increasing support for its additional role in communication. An acoustic analysis of echolocation pulses of the bat *Rhinolophus clivosus* confirmed sex and individual vocal signatures in echolocation pulses. A habituation–dishabituation playback experiment suggested that bats perceived these signatures because listening bats clearly discriminated between the sexes (two classes) and between individuals (representatives of a multiclass category), although to different degrees. The simple acoustic structure of these vocalizations provides sufficient specificity for sex discrimination but has limitations for individual discrimination because pulse parameters of individuals increasingly overlapped with increasing group size. We conclude that selection for the primary function of echolocation restricts the acoustic space available for communication. However, we frequently observed echolocation pulses with conspicuous structural modifications. Statistical analyses revealed that these vocalizations yielded increased individual distinctiveness. Such added systematic variation may indicate a communicative function and perhaps a signalling intent of the emitter, although the latter has yet to be tested. The findings suggest that the required specificity for effective communication could be obtained through modification of echolocation variants when adaptations for orientation and foraging constrain the evolution of complex communication signatures.

Acoustic signals are important vectors in animal communication systems and are used by many group-living taxa to mediate social interactions. A functional communication system relies on unambiguous and specific signals whose coding system is shared between communication partners (e.g. Bradbury & Vehrencamp, 2011). Such communicative specificity is often achieved through the acoustic structure of the signal. Distinct features of the acoustic signal may encode vocal signatures (e.g. species identity), contextual cues (e.g. courtship calls) or arousal states (e.g. levels of urgency). Therefore, an effective communication signal should feature both specificity and structural flexibility to allow the communication of more complex information. This idea has been incorporated in the 'social complexity hypothesis' (see Freeberg, Dunbar, & Ord, 2012; Oller & Griebel, 2008). A corollary to this is that limitations in signal flexibility may limit the complexity of information conveyed. Such limitations may arise, for example, as a result of trade-offs in signals that have more than one function. Multiple functions can arise from the co-option of traits that had evolved in the context of one function being used to serve an additional function.

Co-opted traits that are used in communication are often visual or olfactory signals, for example bird plumage (Cowen, 2005;

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Gluckman & Cardoso, 2010) or urine scent marking (Gosling & Roberts, 2001), respectively. Acoustic signals, on the other hand, have almost exclusively evolved for communication and therefore co-option of vocalizations for additional functions are rare. Two exceptions to this are sounds emitted by some insects and echolocation pulses emitted by bats. For example, the ultrasonic clicks of some moths in the subfamily Arctiinae evolved in response to bat predation (e.g. Dunning, Acharya, Merriman, & Ferro, 1992; Jacobs & Bastian, 2017; Miller, 1991) but have apparently been co-opted for use in intraspecific communication (e.g. Sanderford & Conner, 1990). Bats and dolphins (and a few bird species and shrews) use acoustic signals for orientation and foraging in the form of echolocation (Brinkløv, Fenton, & Ratcliffe, 2013; Siemers, Schauermann, Turni, & von Merten, 2009; Thomas, Moss, & Vater, 2004) and recent research has suggested that bat and dolphin echolocation may also be used in communication (e.g. Gregg, Dudzinski, & Smith, 2007; Jones & Siemers, 2011); thus, it might be a trait with two functions. In multifunctional traits, one or more functions may be limited from exhibiting an optimum adaptive response (Hansen, 2015). That is, optimization of the trait for one function may limit optimization of that trait for the other function/s, resulting in a trade-off (Garland, 2014). In the case of bat echolocation, acoustic signals that have primarily been selected in the context of orientation and foraging may not have the requisite structural flexibility of communication signals. Echolocation therefore provides an excellent opportunity to study signal design in general and the association between structural complexity and communicative versatility.

Among the different types of echolocation systems that evolved in bats, high duty cycle echolocation (HDC; relatively long pulse durations compared to silent periods between pulses) is a specialized form of echolocation that enables bats to detect small flying insects even within dense vegetation using only acoustic cues (Schnitzler & Denzinger, 2011). These echolocation pulses are characterized by a long constant frequency component (CF) of narrow bandwidth which is flanked by frequency modulated sweeps (FM) of broad bandwidth. The FM components allow precise range determination and exact target localization through neuronal processing of the time elapsed between the emission of the pulse and the return of the echo (Simmons & Stein, 1980). Echoes of the CF component carry information about the target via acoustic glints. When the CF component reflects off the fluttering wings of an insect, the returning echo carries distinctive peaks in frequency and intensity, the so called ‘acoustic glints’. These glints are caused by Doppler shifts in frequency as a result of the motion of the wings and changes in the effective reflective area of the wings when they are at different angles to the impinging echolocation pulses, respectively (Neuweiler, 2003). Although these glints can be minute, down to ±20 Hz modulation depth (Ostwald, Schnitzler, & Schuller, 1988), bats obtain detailed information about the target velocity and direction of movement (Neuweiler, 1990). The long duration of the CF component enables these bats to discriminate between different types of insects by analysing the pattern of sequential glints caused by distinct wing beat cycles (Nachtigall & Moore, 1988). Furthermore, the frequency of the CF component is tightly linked to the specialized auditory pathway of these bats which contains an ‘auditory fovea’. The fovea is an area of increased sensitivity and high resolution of a narrow range of frequencies that can detect and integrate the minute modulations of the glints (Neuweiler, 1990). Thus, the relatively simple acoustic structure of FM-CF-FM echolocation pulses is adapted to the central perceptual tasks associated with habitat and foraging mode (Schnitzler & Denzinger, 2011). This structural optimization may constrain the encoding of additional vocal cues and thus the communicative function of these vocalizations.

Nevertheless, echolocation is consistently discussed in a communication context (e.g. Barclay, 1982; Heller & von Helversen, 1989; Siemers, Beedholm, Dietz, Dietz, & Ivanova, 2005). The assumption of a dual function is supported by (1) the ability of bats to eavesdrop on echolocation pulses of other bats to extract information about e.g. feeding sites, (2) the occurrence of private frequency bands between sympatric species and (3) the existence of self-reporting signatures in echolocation pulses (see Jones & Siemers, 2011 for an overview). The fact that echolocation pulses of some species carry intra- and interspecific signatures encoding attributes of the emitter such as age or species affiliation (reviewed in Jones & Siemers, 2011) makes them candidates for communication signals. Recent playback experiments provide evidence that HDC bats can perceive these vocal signatures by discriminating between species, populations, the sexes and body condition on the basis of echolocation alone (Bastian & Jacobs, 2015; Knörnschild, Jung, Nagy, Metz, & Kalko, 2012; Lin, Liu, Chang, Lu, & Feng, 2016; Puechmaille et al., 2014; Schuchmann, Puechmaille, & Siemers, 2012; Voigt-Heucke, Taborsky, & Dechmann, 2010).

Our aim in this study was to test the limitations that multifunctionality and the potential resultant trade-offs impose on acoustic signals, particularly in a communication context. We proceeded by selecting categories of information (such as sex and individual identity) that are likely to be informative for bats in a communication context and likely to be represented in echolocation pulses by vocal signatures. Vocal signatures can represent different levels of recognition entities, ranging from e.g. species to group and down to individual recognition. Each level contains a different number of classes that need to be discriminated if signatures are to be reliable identity cues. We chose sex and individual as categories as they differ in the number of classes they contain. We experimentally tested the perception of the signatures of sex (male versus female, two-class category) and individual identity (pairwise tests of three random individuals from a pool of many individuals, representative of a multiclass category) by listening bats. We then compared the distinctiveness of the two-class category of sex with the multiclass category of individual identity based on the acoustic structure of the emitted vocalization.

Our model species, Geoffroy's horseshoe bat, *Rhinolophus clivosus*, like other species of horseshoe bats (Rhinolophidae), uses high duty cycle FM-CF-FM echolocation pulses. It roosts in groups of variable numbers of conspecifics comprising tens to hundreds of individuals with seasonally fluctuating sex ratios (McDonald, Rautenbach, & Nel, 1990; Monadjem, Taylor, Cotterill, & Schoeman, 2010). It also occurs sympatrically and syntopically with other species of horseshoe bats (Monadjem et al., 2010; Schoeman & Jacobs, 2011). Accordingly, it has been repeatedly shown that horseshoe bats can discriminate between their own species and heterospecifics based on echolocation pulses (Bastian & Jacobs, 2015; Li et al., 2013; Schuchmann & Siemers, 2010). Therefore, species-specific communication channels might be important in this species making it well suited for investigating limitations imposed on a communicative signal as a result of multifunctionality. Recent research (Raw, 2016) indicates that species discrimination is based on a single-class category level, i.e. the recognition of its own species. A potentially meaningful two-class category is sex, where differences in acoustic structure exists between two states, male and female. Acoustic sex identification is found in various vocalizing taxa including insects (von Helversen & von Helversen, 1997), birds (Cure, Aubin, & Mathevon, 2011; Stirnemann, Potter, Butler, & Minot, 2015) and